Biology of *Morpho polyphemus* (Lepidoptera: Morphidae) in El Salvador

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Abstract: This paper summarizes various studies on the biology of *Morpho polyphemus* (Lepidoptera: Morphinae) in El Salvador. Emphasis is placed upon the interpretation of observed life cycle, larval host plant specificity, parasitism of eggs and larvae, larval behavior, and adult behavior in terms of a generalized adaptive evolutionary strategy that accounts for the ability of this butterfly to successfully colonize isolated patches of second-growth forest. In Central American countries the butterfly is generally confined to the canopy of undisturbed primary-growth rain forest (Costa Rica). In El Salvador, where virtually all primary-growth forest has been destroyed through land-clearing agricultural practices (slash-burn systems), the species has survived in small second-growth habitats where a major larval host plant, *Paullinia pinnata* (Sapindaceae), is abundant. Comparisons of development time with two subspecies of *Morpho peleides*, indicate that the ability of *Morpho polyphemus* to survive in second-growth forest communities is a relatively recent event. Various hypotheses are advanced to account for observed seasonal differences in adult abundance since the dry season is pronounced at the study site.

Herein we describe the biology of *Morpho polyphemus polyphemus* (Morphinae) in El Salvador for this Central American species, which, according to various authors (e.g., Seitz, 1924; Le Moult and Real, 1962) has previously been undescribed. We also summarize the first records of larval host plants, and notes on the ecology and behavior of adults and immatures. This paper is one of a series on the biology of Central American *Morpho*.

Our ultimate goal in studying the biology of Central American *Morpho* is to account for the evolutionary biology of the genus as a whole. In this paper we hypothesize about the evolutionary history of *Morpho polyphemus*, relative to its presumed South American heritage with the *catenarius* series (Seitz, 1924) and in contrast with a sympatric species, *Morpho peleides hyacinthus*.

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FIG. 1. Life cycle of *Morpho polyphemus*. Vertical column (from top to bottom):
eggs (as laid in the laboratory); first instar larva, dorsal aspect; third instar larva, lateral
aspect. Single right photograph: third instar larva, dorsal aspect.

HABITAT AND STUDY PROCEDURES

All field studies were made in heavily-disturbed early second-growth seasonal
tropical wet forest forming a narrow strip of dense vegetation along the banks of
a small stream running through the village of Barranca Colonia Campestre

(800 m. elev.) in the northeastern sector of San Salvador. Although we have observed *Morpho polyphemus* occurs in heavily-disturbed forest from sea level to 1800 meters (Cerro Verde and Sierra Apaneca), we noted (from 1968 to 1971) that the butterfly is locally common at Barranca Colonia Campestre, and therefore, we have concentrated our studies at this locality. We realize that the various aspects of its biology (most notably host plant specificity of larvae) may vary greatly with geographical and topographic factors.

Our study site consisted of a section of shallow ravine (about 30 m. deep) with the stream (quebrada) running through in an east-west direction. One of the most striking features of this particular study site, and one which we believe may act as a major selective force of the local adaptations of *Morpho polyphemus*, is the high density of human habitation situated along the ridges of the ravine at Barranca Colonia Campestre. Houses and cleared patches of land were only a few meters from the beginning of the second-growth strip which covered the sides of this ravine. The vegetation associated with the sides of the ravine, and in which oviposition by *Morpho polyphemus* was commonly seen, formed a thick layer of undergrowth.

Morpho polyphemus in this area of El Salvador is a typical component of the butterfly fauna associated with cleared areas with breeding activity restricted to the dense, shaded second-growth vegetation that tracks streams in ravines. The undergrowth apparently results from the high sunlight intensity through-out most of the year because a tall, overshadowing canopy (Odani, 1963) is lacking. The original habitat of *Morpho* butterflies in El Salvador has been severely reduced and modified as a result of massive land clearing efforts by man.

Studies conducted include: (1) collection of eggs and larvae for laboratory rearing, (2) records of larval host plant specificity in the field, (3) feeding experiments in the laboratory, (4) observations on predators and parasites on eggs and larvae in the field, and (5) notes on behavior of larvae and adults in the field. Observations were also made on seasonal abundance of adults at the study site. For laboratory rearing studies, cultures of *Morpho polyphemus* were usually maintained in tightly-sealed clear plastic 8″ by 12″ bags.

RESULTS

The results of field and laboratory observations on the biology of *Morpho polyphemus* are summarized below, in the following order: (1) life cycle, (2) host plant specificity, (3) mortality factors, (4) larval behavior, and (5) adult behavior.

Life Cycle: Life cycle studies were concerned with development time from egg to adult and description of life stages. The development time, and size of various stages are summarized in Table 1. The mean development time is about 127 days.

TABLE 1. Some life cycle statistics of *Morpho polyphemus* in El Salvador.[a]

Statistics	Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar[c] 5	Pupa	Total Time Egg-adult
Mean duration (x̄ ± S.E.) in days	11 ± 0.5	8 ± 1.0	9 ± 0.5	14 ± 1.0	23 ± 1.0	35 ± 1.5	20 ± 1.0	126.5
Mean size[b] (x̄ ± S.E.) in mm.	1.9 ± 0.5	9 ± 0.4	15 ± 0.2	35 ± 0.5	40 ± 1.0	71 ± 5.5	30 ± 0.5	—
Mean head capsule width (x̄ ± S.E.) in mm.	—	1.8 ± 0.2	2.5 ± 0.1	3.2 ± 0.1	5.2 ± 0.1	7.2 ± 0.2	—	—
N[d]	140	19	19	13	13	11	11	—

[a] All measurements were made in the same laboratory.
[b] Refers to diameter for egg, and body length (head-tail) in larvae and pupae.
[c] Instar 5 includes an active non-feeding prepupa which lasts 2–3 days.
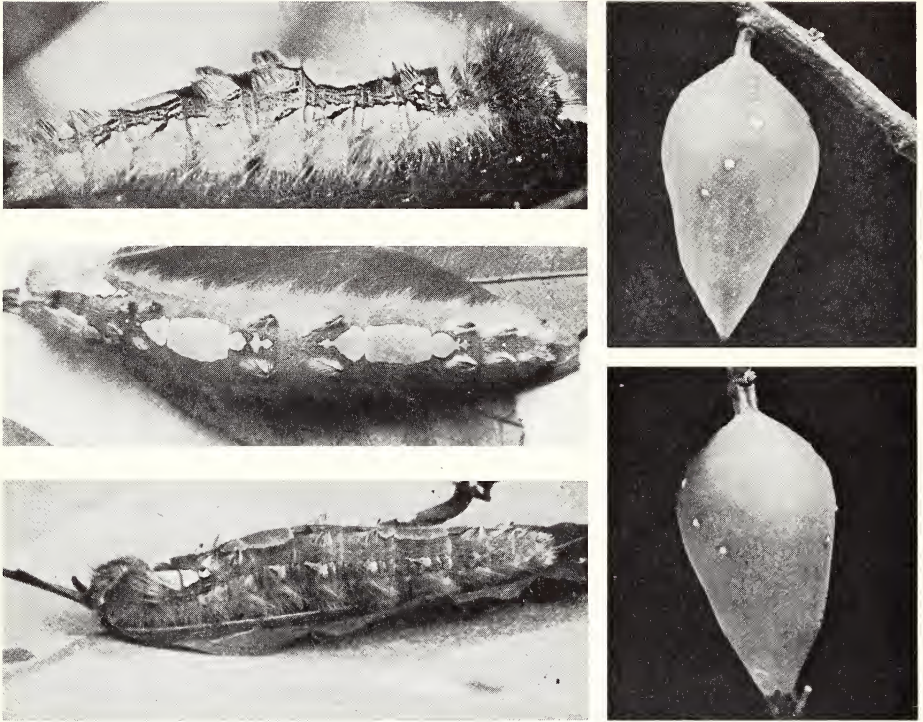[d] N is the number of individuals measured.

Fig. 2. Life cycle of *Morpho polyphemus*. Left vertical column (top to bottom): fourth instar larva, lateral aspect; fifth instar larva, dorsal aspect; fifth instar larva, lateral aspect. Right column: pupa, lateral aspect; pupa, dorsal aspect.

The egg, when first laid, is light green but soon (2–4 days) develops a noticeable broken dark brown band outlining the lid through which the first instar larva will emerge (Fig. 1). Near hatching time, the egg turns dark reddish-brown and the larva (especially the head) is clearly visible inside. In the field, eggs are usually laid singly, although occasionally an ovipositing female will deposit from 1–4 eggs on a single leaf of the host plant; however, in such unusual instances, the eggs are never clustered (i.e., touching one another), but rather scattered on the dorsal surface of the leaf. Occasionally a female will oviposit several eggs within a cluster of leaves on a single host plant. Eggs are affixed to the dorsal surface of a leaf but the actual site on the leaf is seldom consistent (i.e., eggs are not always laid near the edge of the leaf, etc.). Eggs are usually laid on the older leaves of the host plant.

First instar larvae (Fig. 1) devour their empty egg shells immediately upon hatching and then move to the ventral surface of the leaf. The body of the first instar is white interspersed with large patches of red dorsally, which are connected laterally by a thin line on each side. Hairs projecting dorsally are black, while lateral hairs are white (Fig. 1). The head is broader than the width of

the body and is reddish-brown with multiple rows of black hairs along the lateral and dorsal edges. The entire surface appears finely pitted and possesses reflective properties. The ventral portion of the body is translucent greenish-white.

The second instar closely resembles the first instar, although pairs of thin tufts of white hair now appear dorso-laterally on segments 1, 4, and 7; the tufts associated with segment 4 are longer than those of segments 1 and 7. The appearance of these tufts represents the appearance of a *Morpho* character that persists and is further developed in later instars. The second instar is generally the same color as the first instar, with the single noticeable exception being the possession of reddish hairs on the head where the black hairs had been in the first instar. These hairs are also shorter than in the first instar.

It is during the third instar (Fig. 1) that the larva takes on a markedly different external appearance. First, the general body color becomes gray-grown and infiltrated by a network of light yellow lines bordered with black. The dorsal white patches of the first and second instars now take on a yellowish-green color with their outlines more well-defined by a pronounced border of black (Fig. 1). The larva no longer appears red and white but grayish-brown with two prominent yellow-green spots. The head becomes hairy, with hairs now arising from frontal regions in addition to the lateral edges. The head is now light brown in color and the hairs are silvery-brown in color. There is a noticeable increase in numbers and lengths of hairs associated with the false and true feet, at the latero-ventral edge along each side of the body; these hairs appear as loose brushes arising directly opposite the feet and directed downward, giving the appearance of a series of small brushes obscuring the ventral edges of the body. These hairs are light silvery-brown in color. There is the appearance of new pairs of tufts, on segments immediately behind those in which tufts were already present in the second instar. Therefore, the tufts appear as double sets, arising from segments 1 and 2 (first doublet), segments 4 and 5 (second doublet), and segments 7 and 8 (third doublet). While each tuft is thicker than those of the second instar, they are also shorter in length and take on a "chopped-off" appearance. However, the tufts of the first doublet remain long and directed forward towards the head (Fig. 1), while the remaining two doublets are directed upwards. The latter two sets of tuft doublets are purplish-brown in color while the longer first doublet is light brown.

The tufts comprising the first doublet arise from the anterior edges of segments 1 and 2, while tufts of the more posterior sets arise from the center of their segments. During the fourth instar (Fig. 2), a new doublet of small tufts appears from the middle of segments 2 and 3, and a single new pair of very small tufts appears on segment 9. All tufts are generally light brown and the lateral regions of the body become light yellow-green, like the two major dorsal patches (Fig. 3). The formerly grayish-brown regions of the body now become a more uniform brown color, with less interspersion of lighter lines as seen in the third

Fig. 3. Life cycle of *Morpho polyphemus*. Above: female, dorsal aspect. Below: female, ventral aspect.

instar. The head retains its light brown color, but the frontal region takes on a cream color in the form of an isosceles triangle with the apex continuing back along the head suture as a faint cream-colored line. The head retains the hairy condition of the third instar.

The fifth instar larva is generally a pale brown color, with the formerly yellow-green patches of the dorsal region now uniformly light green (Fig. 2). The dorsal patches have also become further subdivided into small isolated dorso-lateral (segment 2) or dorsal (segments 5, 9) irregularly-shaped spots of bright green. The tufts, with the exception of the first doublet, are now greatly reduced in length and thickness, and in conjunction with a reduction in the thickness of tufts associated with the legs, give the larva a generally smooth appearance unlike the previous instars. The hairs on the head are reduced in number and are generally of a finer texture than in previous instars. The lateral rather continuous yellow-green stripes of the fourth instar are now reduced to small patches (one per segment) of bright green (Fig. 2). Tufts of the first doublet remain long and filamentous, and directed horizontally towards the head. At this instar, the larva appears to be a light brown object and takes on a more cryptic appearance than the previous instars.

About 2–3 days prior to pupation, the larva changes to a light green color all over, with only the head and tufts of hairs remaining brown in color; this is an active prepupa stage characterized by increased locomotor activity resulting in dispersion of larvae from the host plant, and by the complete cessation of feeding. The wandering prepupa eventually pupates in nearby heavily-shaded undergrowth, with the resulting pupa being uniformly light-green (same color as the prepupa) with the major markings being the yellow spiracle opening (Fig. 2). The pigmented spiracle openings are largest on the most anterior segments and gradually being reduced in size to the cremaster, which is bluish-green. The anterior end of the pupa is strongly forked with the paired projections being tipped in wine red. There is no noticeable change in the coloration of the pupa as the adult develops, although usually within 24 hours of eclosion, it darkens slightly. The pupa is very cryptic in appearance since larvae usually pupate on stems and leaves of vines and shrubs in heavily-shaded undergrowth. Empty pupa shells remain intact for several months in the field, making it easy to estimate local abundance of the species. Empty pupa shells were found close to host plants containing eggs and first instar larvae, suggesting that the ravine at Barranca Colonia Campestre is a major breeding site for *Morpho polyphemus* throughout the year.

Adult *Morpho polyphemus* exhibit little sexual dimorphisms in body and wing coloration (Figs. 3–4), although males are generally smaller than females in terms of average wingspan. Neither Seitz (1924) nor Le Moult and Real (1962) allude to sexual differences in this Central American *Morpho*. We observed that one sexual difference is the pronounced submarginal row of crescent-shaped black spots on the dorsal surface of the hindwings in females (Fig. 3),

FIG. 4. Life cycle of *Morpho polyphemus*. Above: male, dorsal aspect. Below: male, ventral aspect.

which is almost totally absent in males (Fig. 4). With respect to ventral markings of the wings, the submarginal series of small ocelli of the hindwing (yellow, ringed with black) is more complete in the female (Fig. 4). General wing coloration both ventrally and dorsally ranges from white to pale greenish white in most specimens at the study site; wings are highly translucent so that ventral ocelli are usually visible dorsally (Figs. 3–4). *Morpho polyphemus* is morphologically unique from any other species of Central of South American species of the genus because of paucity of scales on the wings, permitting well-developed translucence. Males develop faster than females, by about 1–2 days, as commonly occurs in many species of butterflies.

Host Plant Specificity: At Barranca Colonia Campestre, the major larval host plant is *Paullinia pinnata* L. (Sapindaceae). This plant grows as a tall wiry shrub along the stream edges at the bottom of the ravine. Here, it is exceedingly abundant along sections of the stream, and grows both in sunny as well as heavily-shaded areas. Larger plants tend to lean over the water, sometimes actually having the tips of branches submerged, especially during the wet season (May–October). It is evident that this species forms a major component of the secondary-growth plant community associated with the edge of the stream. Occasionally larvae of *Morpho polyphemus* were found on seedlings of an unidentified species of *Inga* (Leguminoseae) which form a minor part of this plant community. Another legume, *Machaerium salvadorensis* is also abundant at this site, where it grows as a large sprawling armed liana, sometimes growing over *Paullinia*. This legume is the major larval host plant of *Morpho peleides hyacinthus* at this site. Neither eggs nor larvae of *Morpho polyphemus* have ever been found on *Machaerium salvadornesis* at this site, despite intensive searching. Larvae of *Morpho peleides* have never been found on *Paullinia pinnata* at this site, although in the laboratory, both species of *Morpho* readily feed and develop on each others host plant. We also observed that *Morpho polyphemus* from the study site completes its development when fed a species of *Inga* from Costa Rica. A few larvae of *Morpho peleides* were found on the same species of *Inga* at the study site. Other host plants have not been found to date, although from study of *Morpho peleides* in Costa Rica (Young and Muyshondt, 1972), we suspect broad larval host plant specificity. In light of our prediction of broad larval host plant specificity in this butterfly, surprisingly we have not found eggs and larvae of it in *Paullinia fuscescens*, which is almost as abundant as *P. pinnata* at the study site. Furthermore, we have consistently failed to find *Morpho polyphemus* on other genera of Sapindaceae also abundant at the study site, most notably *Serjania* and *Urvillea*.

Mortality Factors: Preliminary findings on rates of mortality in natural populations of *Morpho polyphemus*, suggest that mortality due to parasitism may be high. Out of 47 eggs collected in a few days at the study site, 27 produced wasps of the genus *Ooencyrtus* (Encyrtidae), a genus noted to parasitize aphids

and to reproduce by polyembryony. Since it has been noted that a single egg of members of the Encyrtidae gives rise to individuals of only one sex (Leiby, 1929), the observed emergence of both males and females of *Ooencyrtus* from a single egg of *Morpho polyphemus* indicates that at least two eggs of the parasite were initially oviposited. No other egg parasite has been found to date.

We estimate levels of larval mortality as high as 50% to be due to parasitism by a species of tachinid fly in the genus *Zenillia*; this figure is based on field samples collected over a two-year period, in which data was pooled to obtain a gross estimate of mortality from this parasite. To date, we have only one species of *Zenillia* recorded for this *Morpho* at the study site. Like many species of tachinids, the species of *Zenillia* which attacks the larvae of *Morpho polyphemus* does so by ovipositing eggs on leaves of the host plant, which are then ingested by the feeding host larvae.

We have failed to observe predation on eggs and larvae in the field and we suspect that predation by ants and other leaf-wandering forms is low.

In the laboratory, large numbers of larvae die in later instars from what appears to be a form of virus intestinal infection, resulting in discharge of large amounts of partially-digested leaf material. We do not know if such mortality occurs in the field, although we suspect that it does since such a disease is probably transmitted on leaves of the host plant.

Estimation of survivorship of adult *Morpho polyphemus* has not been studied, although we are planning an extensive mark-recapture program to study mortality on adults.

Larval Behavior: Larvae always occur singly in the field, with no indications of gregarious behavior, so well observed in other species of South American *Morpho*. During the first four instars, larvae remain on the ventral surfaces of older leaves of *Paullinia*. Here, each larva builds a thin silken mat which functions as both an anchoring device during resting periods as well as during periods of molting. Larvae only leave their silken resting mats for feeding episodes. Although we have not yet studied the diurnal feeding pattern in the larvae of *Morpho polyphemus*, we know that the larvae of *Morpho peleides* are strictly "dawn-dusk" feeders. We suspect that feeding in larval *Morpho polyphemus* may be either nocturnal or of the "dawn-dusk" variety, since both forms of behavior have been noted for the genus (Seitz, 1924; M. Barcant, pers. comm.; L. S. Otero, pers. comm.). Our field observations rule out diurnal feeding in this species.

Fifth-instar larvae rest on heavily-shaded branches of the host plant, lower than the leaves where they concentrate the bulk of their feeding. In such a resting position, the crypsis of the coloration of the fifth instar becomes evident. Fifth instars also construct resting mats along the branches. Sometimes, fifth-instar larvae appear to be aggregated on branches. We interpret this as a result of a shortage of space when several such larvae occupy an individual host plant,

rather than as a coordinated behavioral pattern in which larvae collectively congregate and exhibit collective responses for feeding, defense, etc.

We have conducted some preliminary tests on the defense systems of larvae—especially fourth and fifth instars. When initially prodded with small bristle brushes, a larva responds by violent pushing and waving movements of the anterior region of the body. When this is repeated several times within a few seconds, the larva raises the anterior end of the body and everts a small orange gland from a slit located between the first pair of true legs; a strong odor similar to that of rancid butter is emitted apparently from this everted gland. We interpret this as a chemical defense system perhaps similar to those known for certain papilionid butterflies and noctuid moths (Eisner, 1970). We have not studied this defense system outside of the laboratory, nor have we yet studied it with simulated attacks by ants, in the laboratory. Such studies, however, are planned.

The larvae of *Morpho polyphemus* exploit three systems of defense that follow in sequence: (1) strategy of hiding underneath leaves and on shady branches, (2) violent physical movements upon initial contact with a potential predator, and (3) the bringing into operation of a chemical system of defense when the first two strategies fail to deter the attacker.

Adult Behavior: Our major observations on behavior patterns of the adults concern movements of ovipositing females at the study site. Females generally oviposit in the early afternoon (12:30–2:00 P.M.) and reproductive effort (Labine, 1968) tends to be concentrated over small sections of the habitat. A single female will soar down the side of the ravine where *Paullinia* is abundant, and lay several eggs encompassing a few oviposition sequences within a small area. Such oviposition episodes are repeated several times by the same female, interrupted by short periods of resting in tall trees. While we have no data on the vagility of fecundated females, we believe that individuals will often deposit a large number of eggs in a given area where the host plant is abundant; whether or not the same female returns on several days to the same spot for oviposition cannot be ascertained. We do know that such behavior commonly occurs in *Morpho peleides* in Costa Rica. Elucidation of such behavior and how it contributes to the distribution of reproductive effort in space is an important aspect of understanding the evolutionary biology of the species. With respect to fecundity, females dissected immediately after eclosion usually contain about 15 eggs, while females captured in the field may contain as many as 80 eggs. Egg maturation probably peaks in *Morpho polyphemus* following insemination.

During oviposition, the female grabs the petiole of the leaf, holds her wings partly closed, and deposits the egg. Eggs are firmly attached to the dorsal surfaces of leaves, and are not easily dislodged. We suspect that oviposition is accurate in this species, with minimal erring known to occur in other species of butterflies (Dethier, 1959). There is no consistent pattern with respect

to site-selection on an individual *Paullinia* bush since an individual female may oviposit on leaves near the top as well as on leaves near the bottom of the bush. However, eggs are always laid on older leaves. We noted similar oviposition site-selectivity in *Morpho peleides* (Young and Muyshondt, 1972).

While adults of both sexes are presumably vagile in their daily movements, they are most abundant at three different times of the year: December– January, April–May and August–September. The adult population present during April–May, the beginning of the wet season, is the largest of the three peak abundances, being about four times as large as the smallest peak which occurs during the dry season (December–January); the remaining peak, which we term "moderate," occurs during the wet season (August–September) and is about one-half the size of the peak occurring during April–May. Our estimates of adult numbers are taken from daily records taken several times each month at the study site, and entail intensive search periods for about one hour each day. Marking studies, however, have not yet been conducted.

DISCUSSION

We feel that our observations on *Morpho polyphemus* are best discussed in terms of the following considerations intimately associated with the biology of the species: (1) sympatry with *Morpho peleides*, (2) effects of habitat destruction, (3) models of seasonal abundance, and (4) an evolutionary adaptive strategy.

Sympatry with Morpho peleides: In another report (Young and Muyshondt, 1972) we summarized the life cycle and biology of *Morpho peleides* in Costa Rica and El Salvador. The El Salvadorian population of this species is sympatric with *Morpho polyphemus* in the ravine at Barranca Colonia Campestre. Both species are common with having two of the four peak periods of adult abundance of *Morpho peleides* coinciding with the two peak periods of adult abundance in *Morpho polyphemus*. Both species oviposit in the ravine but the major larval host plant of *Morpho peleides* is *Machaerium salvadorensis*. There appears to be competitive exclusion so that each species exploits a different host plant for oviposition and larval development. The operation of this ecological process is further suggested by the free cross-feeding of larvae in the laboratory. Both species have the necessary physiological machinery to feed on each other's major local host plant, although ecologically, this does not occur in the field. This difference in larval host plant specificity in the field may be the major mechanism accounting for co-occurrence of the two species at Barranca Colonia Campestre. We emphasize the apparent larval host plant exclusion exhibited by sympatric populations of these two species of *Morpho* since previous host plant records for other species (Seitz, 1924; Costa Lima, 1936; Otero, 1971) do not consider the question of local host plant specificity as related to sympatry among species of the genus. Ehrlich and Raven (1964)

summarize various plant families known to contain host plants for *Morpho*, although again, data are apparently lacking on local host plant lists of sympatric species.

Such niche separation may also operate with respect to adult food sources, although previous study (Young, 1972a) has suggested that sympatric species of *Morpho* are characterized by adult populations exploiting the same food sources, on a regular basis. We have no records on food selectivity in adults of the species in El Salvador.

Morphologically, it is apparent that both species belong to different taxonomic groups within the genus. Seitz (1924) assigns *Morpho polyphemus* to the *catenarius* series, while *Morpho peleides* belongs to the *achilles* group. Both species groups show their greatest speciation in South America while *Morpho polyphemus* represents the single extension of the *catenarius* series into Central America, and *Morpho peleides*, together with a closely related species, *Morpho granadensis*, represents the geographical expansion of the *achilles* group in a similar northward manner. Other expansions of the South American fauna into Central America are represented by *Morpho theseus* (*hercules* group), *Morpho cypris* (*rhetenor* group), and *Morpho amathonte* (*rhetenor* group). Of all six species occurring in Central America, only *Morpho peleides* and *Morpho polyphemus* regularly occur in El Salvador. The remaining species, all of which occur in Costa Rica, are generally confined to undisturbed primary-growth lowland and montane tropical wet forest, a major vegetational habitat virtually extinct in El Salvador. On the other hand, species such as *polyphemus* and *peleides* are considered to be more often associated with second-growth plant communities and represent a major ecological expansion of the genus into such less stable environments. For these reasons, it is of tremendous ecological interest to determine the point of sympatry among the two species, and to contrast their biologies in such habitats.

Morpho peleides is a "brownish morpho" (Young, 1971a) while *Morpho polyphemus* is a "glossy white morpho." Their life stages differ to some degree, especially instars 3–5, and the pupa (see Young and Muyshondt, 1972a). Such differences reflect differences in the evolutionary history and divergence between species. *Morpho peleides hyacinthus* has an average developmental time of 76 days, while a Costa Rican subspecies, *peleides limpida* takes an average of 108 days for development from egg to adult (Young and Muyshondt, 1972a). Both subspecies of *peleides* therefore possess shorter developmental times than *Morpho polyphemus* (120) days, and we speculate that the prolonged ontogeny of this species is a result of a long evolutionary processes involving adaptation to survivorship in more stable plant communities, most notably primary-growth montane tropical wet forest. Adults of *Morpho polyphemus* are significantly larger than adults of *Morpho peleides*, lending further support to the idea that the former species has experienced a long evolutionary history in stable forest

communities; long developmental time and large size are among some of the traits predicted to be characteristic of insect species that are members of stable terrestrial tropical communities (e.g., Margalef, 1968). Seitz (1924) points out that the South American species of the *catenarius* series are typically associated with high altitude "primeval" forests. Furthermore, he mentions that in Central America, *Morpho polyphemus* is often found in areas of high human habitation as well as being a "canopy-dweller" in undisturbed forests. *Morpho peleides* has apparently experienced a long evolutionary history involving geographical expansion into montane forests from lowland forests, and from stable plant communities into highly disturbed plant communities. Such high plasticity with respect to adaptive radiation is implied for other members of the *achilles* group (Blandin and Descimon, 1970). Furthermore, *Morpho peleides* has undergone more extensive adaptive radiation in Central America than has *Morpho polyphemus* as indicated by the occurrence of no less than 17 subspecies of the former species in contrast with only two subspecies of the latter species (Seitz, 1924). A shorter average developmental time is predicted as one of several adaptations to colonization of less stable environments (MacArthur, 1962). Therefore, the invasion by *Morpho polyphemus* into highly disturbed second-growth plant communities represents a recent ecological expansion in evolutionary time, while that of *peleides* is more ancient.

We believe that the successful and persistent concurrence of both species of *Morpho* in a relatively restricted habitat at Barranca Colonia Campestre has been facilitated by differences in the past evolutionary history of each species, in addition to the capacity of each species to exploit different larval host plants. Carrying our argument further, we predict average smaller size in *peleides* than in *polyphemus*, which does occur (average wingspan of male *peleides* is 8.5 $\pm$ 1.4 cm, N = 10; average wingspan of male *polyphemus* is 11.5 $\pm$ 2.0 cm, N = 10), and also higher fecundity in *peleides*, which we have not yet measured in either species. From theory of intrapopulational adaptation to stable environments (e.g., Levins, 1968), we also predict lower genetic variability in *Morpho polyphemus*, which may in fact be undergoing transient polymorphism in response to entering a new adaptive zone.

Effect of Habitat Destruction: Seitz (1924) mentions that *Morpho polyphemus* occurs locally as both a species associated with the canopy of tropical forests, and also near the ground in areas of massive land clearing and human habitation. In light of the fact that the majority of other species of *Morpho* are associated with either understory or canopy of primary-growth forests (with the exception of the *achilles* group), we find this dichotomy in habitat selection of *Morpho polyphemus* of particular interest. Although Seitz mentions that the species occurs at high altitudes (i.e., 1300 m. elev. in Guatemala), we find that it occurs over a wide altitudinal range in El Salvador. Seitz (1924) also points out that the majority of other species of *Morpho* belonging to the same series as

polyphemus (i.e., *perseus, theseus, laertes, catenarius,* etc.) are primarily distributed at high altitudes, where they occur primarily as canopy-dwellers. For example, in Costa Rica, *Morpho peleides* and *Morpho theseus* are sympatric locally at high altitudes (900–1000 m.), although the latter species is strictly a canopy-dweller while the former is common in low second-growth vegetation. All of these species possess white color patterns on their wings, and we argue that such coloration is an adaptation for unpalatable species inhabiting montane or cloud forests, where diffuse light (rather than direct sunlight) permits the exploitation of a color-contrast strategy for advertisement (i.e., white butterfly against dull backgrounds). Such considerations assume that such species of *Morpho* have evolved primarily in primary-growth montane forests, rather than in lowland wet forests, where various forms of bright blue reflective coloration of wings in association with direct sunlight would be a morphological adaptation associated with unpalatability or other predator-escape defense mechanisms (Young, 1971a).

In Costa Rica, the geographical distribution of *Morpho polyphemus* is generally restricted to the hills (200–300 m. elev.) near Rincon on the Osa Peninsula (Puntarenas Province). Here, the species occurs above primary-growth tropical wet forest and is seldom seen at lower elevations near the coast. The canopy of the evergreen forest at Osa typically occurs at 30–45 meters height and this is where adults of *Morpho polyphemus* are usually seen. Baiting experiments on the ground consistently fail to attract adults of this species at Osa, while readily attracting *Morpho peleides*. *Morpho polyphemus* at Osa in every sense of the word appears to be a canopy-dweller. We have consistently failed to find this species in areas of human habitation in Costa Rica, whereas the reverse is true in El Salvador. The geographical distribution of *Morpho polyphemus* in Costa Rica is restricted despite the availability of similar habitats in other parts of the country. We interpret this difference in habitat selection between Costa Rica and El Salvador as the result of recent (about 2,000 years) land clearing movements in El Salvador. The original habitat of *Morpho polyphemus* however is preserved to some degree in Costa Rica.

Depending on the amount and kind of selection pressures operating between Costa Rica and El Salvador, predictions can be made regarding the evolutionary adaptive strategy of the species in both places.

Models of Seasonal Abundance: Adults are most common at the study site three times each year, corresponding roughly to January–February, April–May, and August–September. Many dicots and monocots lose their leaves during the dry season. Others, such as *Paullinia* and *Inga* retain most of their leaves, but become less succulent, and covered with thick layers of dust. Leaves in this condition appear less edible to herbivorous insects. Vegetative growth on *Paullina* and *Inga* is absent during the dry season. The dry season usually falls been late November and early April so that adult *Morpho polyphemus* is most

abundant during the early dry season (December–January), beginning of the wet season (April–May), about mid-way through the wet season (August–September). Each of these three peaks of adult abundance in the ravine varies considerably in magnitude from the others: adults are most abundant at the beginning of the wet season, moderately abundant at the middle of the wet season, and least abundant during the early dry season. Moreover, adults are virtually absent from the study site during intervening months. This apparent seasonal abundance is correlated with its development time: of about four months (Table 1). The peaks of adult abundance fall about four months apart and suggests the occurrence of essentially non-overlapping generations of the butterfly at the study site. Preliminary data on monthly distribution of eggs and various larval instars supports this view.

Seasonal abundance of adults has also been noted for other species of *Morpho*. Seitz (1924) comments that an allied species, *Morpho laertes* which is common in the Brazilian provinces of Rio de Janeiro and Espiruto Santo during January, and steadily declines in numbers towards March. He also mentions that a similar trend takes place for a second allied species of the *catenarius* series, namely *Morpho catenarius*, at Santa Catharina in Brazil. The situation in El Salvador for *Morpho polyphemus* is in part analogous to the situation in Brazil, although data are lacking for peak abundance at other times of the year in the latter situation. Virtually nothing is known about the adaptations of the life cycles in species of tropical butterflies with respect to season variation in rainfall. Therefore, it may very well be that certain species of Brazilian *Morpho*s need at least 10 months to mature so that adults are found at only one time each year. Such an adaptation could evolve as a selective response to regional climatic variation in which a series of short dry seasons ("veranillos") are interspersed with wetter periods, and perhaps one long dry season ("verano"). Selection would tend to favor long development time for species in stable environments (Margalef, 1968; Connell and Orias, 1964; Slobodkin and Sanders, 1969). However, we wish to view the problem in terms of life cycle adaptation to patterns of rainfall.

Many tree species in wet tropical forests become deciduous during periods of high water stress (e.g., Richards, 1952) even though the forest as a whole appears to remain evergreen. Herbivorous insect species feeding on plant species that go deciduous may therefore be temporarily deprived of their food sources. An adaptive strategy for such herbivores would be "switch off" to new host plants that remain evergreen during dry periods, or become metabolically less active until the preferred host plants leaf out again. The latter appears to be the major adaptive strategy for lepidopterous species caught up in such an ecological crisis, since most species are relatively sedentary (on the host plant) during the larval stage. In the specific case of *Morpho*, we have noted that larvae of both *polyphemus* and *peleides* will only eat fresh leaves and reject less succulent and dusty leaves. In host plants such as *Paullinia*, *Machaerium*, and

Inga, leaves appear susceptible to water stress both in the laboratory and in the field. In the field, during the dry season, the majority of leaves on an individual bush or vine of these larval host plants become markedly less succulent and acquire heavy coatings of dust. They therefore appear less palatable to larvae than they do during the wet season. Leaf-fall, however, is spotty in these plants.

We wish to advance several hypotheses that could account for the seasonal abundance of *Morpho polyphemus* in El Salvador. From rainfall data gathered by the Servicio Meteorologico de El Salvador, the pattern of seasonality is generally the same in most parts of the country.

Our first hypothesis has to do with the possible existence of a diapause synchronization in larval populations, as a dry season adaptation. The majority of young larvae present at the beginning of the dry season do not complete development by the December–January adult emergence period, but enter into a diapause condition as their host plants become less succulent. With the beginning of the wet season, these larvae complete development and produce adults. At the same time, adults appearing during December–January lay eggs which hatch, and these larvae also enter into a diapause at the height of the dry season, which normally occurs between February and April. This generation also completes development with the beginning of the wet season, so that the adult emergence at this time is composed of individuals from two generations. The next generation, eclosing in August–September, is smaller since adults are produced from a single generation. Some testable predictions generated by this hypothesis include the following: (1) the adult population present during April–May should be made up of mostly young adults, and (2) there should be a preponderance of fourth and fifth instar larvae during late March and early April as a response to diapause synchronization in the population. An indirect result of diapause synchronization in the larval population may be a reduction in parasitism from tachinids. Decreased larval feeding during diapause would decrease the probability of ingesting tachinid eggs (oviposited on leaves, stems, etc.) assuming that the adult flies actually oviposit during the dry season. As to the possible mechanism initiating a dry season diapause in lepidopterous larvae such as those of *Morpho*, clearly we must rule out any photoperiodic effect comparable to that known for initiation of diapause in temperate zone insects. Since the dry season results in a major physiological change in plants in response to water stress, a possible mechanism for herbivorous insects may involve their response to changes in leaf succulence. This is of particular interest in light of studies on humidity receptors in lepidopterous larvae (Dethier and Schoonhoven, 1968). Increased isolation during the dry season may be another important environmental cue initiating diapause, as this may elevate air temperatures close to the ground. Lepidopterous larvae have been known to initiate feeding in response to changes in air temperature (Dethier and Schoonhoven, 1968).

Another hypothesis concerns massive mortality of larvae from heavy rainfall and stream-flooding at the study site. Many larvae die because of heavy rainfall during September and October, the wettest months of the year, resulting in a smaller number of adults maturing by December–January. Larvae also die from indirect effect of heavy precipitation in the form of mold on eggs and perhaps larvae also. We observed substantial egg mortality due to mold in *Morpho peleides* during the wet season in Costa Rica (Young and Muyshondt, 1972). The major larval host plant, *Paullinia pinnata*, is frequently flooded along the stream edges during the wettest months, and any small larvae present may drown. Such mortality factors would be minimal during the dry season, resulting in a large emergence of adult *Morpho polyphemus* during April–May. Since larvae are in the fifth instar or have actually pupated by the beginning of the wet season they would be relatively unaffected by heavy rainfall. A substantially greater number of larvae should survive at this time. Theoretically the large crop of adults in April–May is the result of a single generation characterized by high survivorship from abiotic mortality factors. Thereafter, rainfall would be more or less moderate throughout the remaining wet season, resulting in some mortality of eggs and larvae, and producing a moderate-sized adult population in August–September. Another possible source of mortality under this hypothesis would be massive mortality of adults during October and November (produced by the August–September emergence peak) due to heavy rainfall, and the inability for adults to mate and oviposit successfully on rainy days of the wettest months of the year. Optimal breeding conditions may be associated with the dry season where flying activity may be maximized. Thus, more females may mate successfully in the adult population appearing at December–January than in adult populations appearing at other times (wet months) of the year.

In a third hypothesis we consider the adverse effect of dryness on oviposition of tachinid flies parasitizing larval *Morpho polyphemus*. The decreased succulence of host plant leaves and the acquisition of dusty coatings on leaves decreases the incidence of successful oviposition by tachinids on these plants; eggs may be less firmly affixed and thus become more easily dislodged during windy periods. *Morpho* larvae feed less on less succulent leaves making feeding more erratic during the dry season. Tachinid eggs are therefore less likely to be eaten before they either desiccate or are blown away. Under this hypothesis, larval survivorship from parasitism is maximal during the dry season resulting in a large cohort of adult butterflies during April–May. A moderate adult population is produced later in the wet season (August–September) presumably since the parasite population is still slowly recovering from its previous massive mortality during the height of the dry season. However, the next generation of adult butterflies (December–January) will be markedly affected by tachinid parasitism, resulting in the smallest peak of adult numbers, since the parasites

are exploiting larvae produced by the August–September adult cohort. The generation(s) of parasites associated with these larvae are presumably able to successfully complete development before the height of the dry season, which begins in early February. The resiliency of the parasite populations to recover after the beginning of the wet season is in part due to new suitable oviposition sites resulting from increased vegetative growth during the wet months.

To account for seasonal differences in peak adult numbers in terms of a massive movement of adult butterflies into the relatively wetter ravines (such as Barranca Colonia Campestre) during the dry season we wish to present a final hypothesis. Adult fecundated females in search of succulent plants for oviposition move into the more humid ravines during the dry season. Since the height of the dry season occurs between February and April, this results in a large adult population resident there by the end of the dry season. We predict that the large adult population present during April–May will consist of old individuals rather than a new cohort of young butterflies as predicted under the other hypotheses. The small adult population occurring during December–January is explained away under this hypothesis by it being a residual population left behind during exodus of many adults out of the ravine before the driest period sets in, presumably a mechanism of population dispersion allowing young adult females to oviposit elsewhere. As the dry season advances, however, the bulk of the adult population contracts in distribution to the humid ravine.

We are at present in no position to support any of the above hypotheses; clearly, more concise assessments of adult numbers, population age-structure, and adult vagility are needed to account for seasonal adult abundance patterns. Any combination of factors relating to the different hypotheses may determine seasonal differences in population productivity.

Regardless of the precise mechanisms accounting for seasonal differences in productivity there is apparent synchronization of highest adult numbers with the beginning of the wet season. For many plant species, the beginning of the wet season is a period of rapid vegetative growth. Therefore, more plant biomass is available to herbivores such as larval *Morpho polyphemus*. Tempered by egg and larval parasitism, the next generation of adults would be of moderate size (August–September), and with decreased vegetative growth at the beginning of of the dry season, population numbers might dwindle due to decreased suitable food supply and parasitism.

Due to observed seasonal patterns of fruit production (Janzen, 1967), we predict that adult food sources would not be a major factor contributing to seasonal differences in productivity. Adults of *Morpho polyphemus* apparently exploit a wide range of fermenting fruits in El Salvador, in addition to decaying fungi. During the short dry season in the Caribbean lowlands of Costa Rica, various species of *Morpho* exploit fallen decaying fruits of *Coumarouna* as a major food source (Young, 1972a, b).

An Adaptive Evolutionary Strategy

We believe that *Morpho polyphemus* represents a species that originally experienced a geographical adaptive radiation into montane tropical wet forests, and subsequently underwent ecological adaptive radiation into less stable second-growth habitats in regions where extensive land clearings by man had occurred over a long period of time.

Central America has experienced extensive and intensive land cultivation practices involving the establishment of monoculture crops, much of which is concentrated in El Salvador (Palerm and Wolf, 1960). The effects of extensive establishment of crop monocultures in the New World Tropics has been recently discussed in terms of the apparent close coevolution between plant species and herbivorous insects characteristic of tropical terrestrial communities (Janzen, 1970). When tropical communities are destroyed (e.g., through primitive slash-burn agriculture systems), many herbivorous insect species confronted with a major ecological crisis, must exploit a more restricted distribution of suitable habitats, or else face extinction. In the case of *Morpho polyphemus*, it is apparent that this species is in the process of adjusting to a very patchy distribution of suitable habitats, most notably those restricted to ravines—the remaining refuge of relatively undisturbed second-growth forest.

We maintain that this ecological adjustment is a relatively recent event which is still evolving. The species in El Salvador no doubt still possesses many of its original ecological and behavioral traits that are in the process of being altered in response to new selective pressures associated with new adaptive zones.

Aside from adaptations associated with life cycle, and seasonality of larval and adult food sources, we believe that another major aspect of the adaptive strategy in this species concerns the evolution and expression of unpalatability.

The evolution of the unique glossy white translucent wings of this species may be an adaptive response for rendering the insect noticeable in the diffuse light so characteristic of montane and cloud forests. Selection favors the advertisement of the butterfly since most individuals in a local population are presumably highly unpalatable as prey for most potential predators. We find some indirect evidence for this in terms of the major larval host plant, *Paullinia pinnata*. Many Sapindaceae have been long suspected of containing noxious compounds in both leaves and bark. Some species of *Sapindus* possess a saponifying glucoside ("saponin") irritating to human skin, while in other species pollen causes severe inflammation of the eyes, throat, and bronchial surfaces. More specifically, for *Paullinia pinnata*, we note, from the *Botanique Pharmaceutique*, a brief comment by Dr. L. Beille, in 1909 (Paris): "L'ecorce contiente un alkaloide: Timboine (Martin, 1877). Elle est acre, irritante. Les graines servent a étourdir le poisson." Translation: The bark contains an alkaloid: Timboine. It is bitter and irritant. The seeds serve to stun fish." An earlier publication in the *Histoire des Plantes* **5**, carried an article by H. Baillon, Paris, 1874, in reference to

Paullinia pinnata: "*Paullinia pinnata* L., espece qui se trouve a la fois en Amerique et dans L'Afrique tropicale, passe, dans ce dernier pays surtout, pour un poison terrible. Les negre emploient sa racine et ses semences. Les indiens qui habitent les forets bresiliennes exprimment, dit-on le suc ses feuilles. . . " . Translation: *Paullinia pinnata* L., a species found both in tropical America and Africa, it is reputed, most of all in Africa, to have a terrible poison. The natives use the roots and seeds. The Indians living in Brazilian forests extract the juice from the leaves. . . " . Such statements suggest medicinal and hunting uses of *Paullinia pinnata* because of its toxic properties. Recently (Levin, 1971), summarizing the adaptive significance of secondary compounds associated with plant species, pointed out that many insect species which feed on plants receive protection against predators in the form of unconverted or converted secondary compounds derived from host plants.

We predict that local larval host plant specificity in *Morpho polyphemus* is narrow; we have only found one species of *Inga* to be a second host plant at the study site. Recently (Brower, 1970), discussed automimicry for other butterflies, and a similar defense strategy may occur in *Morpho polyphemus*. Here, the major host plant, *Paullinia*, is unpalatable while a minor host plant, *Inga*, may be palatable. (Levin, 1971; Whittaker and Feeny, 1971), pointed out that different plant groups vary both qualitatively and quantitatively in the types of secondary compounds they contain. If we assume such differences between *Paullinia* and *Inga*, larvae feeding on these plants may differ in their palatability as prey. This could result in a local population of adult *Morpho polyphemus* being automimetic, primarily of unacceptable individuals (those reared on *Paullinia*) but also including a small fraction being more acceptable (those reared on *Inga*) as prey.

Any unpalatability of *Morpho polyphemus* acquired through feeding on *Paullinia* is most likely a result of modification of some compounds ingested from the host plant. We conclude this from the fact that *Thecla marsyas* which also feed on this plant show a high incidence of hymenopterous parasitism in the larval stage. Such parasites lay their eggs directly on the integument of the host and unless the host possesses an effective defense system, substantial rates of mortality may result. The larvae of *Morpho polyphemus* exhibit defensive movements in addition to cryptic resting behavior, as well as having a chemical defense system. These three devices may lower parasitism rates in natural populations. More data on the mortality rate of insect herbivores associated with *Paullinia* resulting from predation and parasitism, may make it possible to correlate mortality rates with the presence or absence of the butterfly's defense system. It might also be possible to show indirectly that the secondary compounds of *Paullinia per se* do not insure protection against biotic mortality agents. The incorporation and modification of them by the herbivore species as a chemical defense system may account for unpalatability and defense.

South American species of the *catenarius* series exhibit cluster oviposition and larval gregariousness on the host plants (Seitz, 1924; L. S. Otero, pers. comms.). The single Central American representative of this species cluster, *Morpho polyphemus*, consistently exhibits single oviposition and non-gregarious larvae. For example, Luis S. Otero (pers. comms.) has studied *Morpho laertes* in Brazil, and has observed that one female may lay as many as 150 eggs on a few adjacent leaves of the host plant (various species of Leguminoseae). Upon hatching, the larvae collectively remain close together on leaves until the fourth instar, at which time they construct a single continuous silken tent over the extremities of several branches. At the end of the fifth instar, larvae disperse from the host plant for individual pupation. Similar behavior has been noted for *Morpho catenarius* at Rio de Janeiro (Seitz, 1924). Our studies of the allied species, *polyphemus*, show that no such group behavior patterns occur.

Cluster oviposition and larval gregariousness are specialized forms of behavior that must be accompanied by the evolution of effective defense systems. To some extent, the construction of a silken tent in which larvae may rest when not feeding represent a form of behavior related to protection against predators even though younger instars remain exposed to predators and parasites. It is unlikely that only species which exploit unpalatable host plants will be able to evolve larval gregariousness resulting in part, from cluster oviposition. In this way, predators or parasites will be discouraged from attack, as a result of both aposematic coloration of larvae (i.e., red and yellow) and collective movements associated with defense. Such behavior patterns tend to localize breeding populations in stable forest communities since reproductive effort (Labine, 1968) becomes restricted and the distribution of breeding populations is patchy. Such specialization possesses high adaptive value for species inhabiting primary-growth tropical wet forests (Margalef, 1968).

From such considerations, we interpret single oviposition and non-gregarious larval behavior in *Morpho polyphemus*, to be recently evolved forms of adaptive behavior associated with the colonization of less stable environments such as restricted patches of second-growth vegetation. From the theory of *r*-selection (MacArthur, 1962), it is predicted that high adult vagility linked with reproductive patterns that increase population dispersion (i.e., single oviposition as opposed to cluster oviposition) are valuable requisites for successful colonization of less stable (predictable) environments. The geographical distribution of South American species in the *catenarius* series is generally restricted to primary-growth montane wet forest, realized to some extent for *Morpho polyphemus* in Costa Rica, but lacking in El Salvador. Such environments are generally considered to be more stable since they represent later stages in the ecological succession of plant communities. The formation of less stable environments through the impact of man on tropical terrestrial ecosystems has meant that species such as *Morpho polyphemus*, formerly so well integrated into stable

forest communities, had to undergo a major directional shift (i.e., from K-selection to *r*-selection—MacArthur, 1962) in adaptive evolutionary strategy in order to cope with problems of survivorship in less stable environments. Through an evolutionary history entailing exploitation of unpalatable larval host plants and the development of defense systems (larval gregariousness, larval defense movements, and chemical systems of defense) and automimicry, species such as *Morpho polyphemus* could make the appropriate adaptive shifts in ecological and behavioral traits associated with entering less stable adaptive zones. Presumably these traits involved the evolution of single oviposition, nongregarious larval behavior, well developed chemical systems of defense, shorter development time, higher fecundity, and perhaps broader host plant specificity.

An alternate explanation for the colonization of second-growth plant communities by *Morpho polyphemus* would concern severe competitive interaction with other species of *Morpho* associated primarily with the canopy of primary-growth forests, i.e., Central American species of the *rhetenor* group (*Morpho amathonte, Morpho cypris*). We rule this out primarily on the basis of the persistent co-occurrence of all three canopy species on the Oso Peninsula in Costa Rica. Presumably a major mechanism for this concurrence is divergence in larval host plant specificity. Further study of the biology of all three species at Osa in Costa Rica should elucidate such a mechanism if in fact it exists.

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